The importance of alternative host plants as reservoirs of the cotton leaf hopper, *Amrasca devastans*, and its natural enemies

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Abstract

Many agricultural pests can be harboured by alternative host plants but these can also harbour the pests' natural enemies. We evaluated the capacity of non-cotton plant species (both naturally growing and cultivated) to function as alternative hosts for the cotton leaf hopper *Amrasca devastans* (Homoptera: Ciccadellidae) and its natural enemies. Forty eight species harboured *A. devastans*. Twenty four species were true breeding hosts, bearing both nymphal and adult *A. devastans*, the rest were incidental hosts. The crop *Ricinus communis* and the vegetables *Abelomoschus esculentus* and *Solanum melongena* had the highest potential for harbouring *A. devastans* and carrying it over into the seedling cotton crop. Natural enemies found on true alternative host plants were spiders, predatory insects (*Chrysoperla carnea,* Coccinellids, *Orius* spp. and *Geocoris* spp.) and two species of egg parasitoids (*Arescon enocki* and *Anagrus* sp.). Predators were found on 23 species of alternative host plants, especially *R. communis*. Parasitoids emerged from one crop species (*R. communis*) and three vegetable species; with 39% of *A. devastans* parasitized. We conclude that the presence of alternative host plants provides both advantages and disadvantages to the cotton agro-ecosystem because they are a source of both natural enemy and pest species. To reduce damage by *A. devastans* we recommend that weeds that harbour the pest should be removed, that cotton cultivation with *R. communis*, *A. esculentus* and *S. melongena* should be avoided, that pesticides should be applied sparingly to cultivated alternative host plants and that cotton crops should be sown earlier.

Key words: *Amrasca devastans*; survey; population density; plant characteristics; natural enemies

Key message:

- The relative advantages and disadvantages of alternative host plants (as sources of both pests and their natural enemies) near crops are likely to vary across agro-ecosystems.
- In cotton, alternative host plants (both weeds and cultivated species) harbour herbivorous pests, in particular during the inter-harvest period, but also harbour beneficial predators and parasitoids.
- Pest damage would likely be reduced if weeds were removed and intercropping with vegetables avoided. Adjusted sowing regimes could reduce vulnerability of seedling crops to high pest densities.

Author contribution statement: R. Saeed gathered the data, analysed the data and wrote the manuscript. M. Razaq instigated the research and commented on the manuscript. I.C.W. Hardy analysed the data and wrote the manuscript.

Introduction

Agricultural production is commonly, and negatively, affected by insect pests (Kogan and Jepson 2007; Gray et al. 2009) and the problem can be exacerbated by agro-intensification due to rapidly growing human populations (Goodell 2009; Carriere et al. 2012). Some phytophagous pests attack only a single cultivated plant species (monophagy) (Forare and Solbreck 1997), while others have a wider range of host plants (polyphagy) including cultivated plants and species which are not under agricultural production (Li et al. 2011). Ascertaining the importance and extent of alternative host plants, both naturally growing and cultivated, can be fundamental to preventing the development of polyphagous pest populations on a ‘main’ or ‘focal’ agricultural species (Tabashnik et al. 1991). For instance, alternative host plants can support reservoirs of pests during periods when main hosts are seasonally unavailable, with pests subsequently migrating back onto the main host plants (Clementine et al. 2005). Alternative hosts plants can also be agriculturally beneficial when they harbour populations of natural enemies (Naveed et al. 2007). Thus, the availability, density and type of alternative host plants (Power 1987; Atakan and Uygur 2005), and the prevalence of natural enemies (Koji et al. 2012) can be important factors influencing the damage caused by insect pests. Due to the great diversity of agricultural systems, and species involved, the relative advantages and disadvantages of the presence of alternative host plants in the vicinity of crops is likely to vary across agro-ecosystems.

The cotton leaf hopper, *Amrasca devastans* (Dist.) (=*Amrasca biguttula biguttula* (Ghauri 1983)) (Homoptera: Ciccadellidae) sucks sap from plant leaves and also injects toxic saliva, which can cause stunted plant growth, with leaves curling downwards and becoming yellow and then brown and dry, and, in severe cases, the shedding of fruiting bodies (Rehman 1940; Narayanan and Singh 1994). *Amrasca devastans* has been regarded in the Indian subcontinent as the most common and most devastating major insect pest of cotton (*Gossypium hirsutum* L.) since the first quarter of the 20th century: reported cotton yield losses range from 37-67%, respectively (Ahmed 1982; Ahmad et al. 1985; Bhat et al. 1986) and crop failure can be complete in given localities (Rao et al. 1968). Farmers in this area rely only on chemical pesticides to manage *A. devastans* (Yousafi et al. 2013; Razaq et al. 2013), even though frequent spraying is likely adversely affect the natural enemy fauna (Zidan 2012).

Amrasca devastans is not limited to feeding and breeding on cotton plants: it is regarded to be a widely polyphagous herbivore that can remain active throughout the year due to the continuous availability of alternative host plants. In many cotton growing areas in Asia, such as Pakistan, agricultural practices have changed from mono-cropping to multi-cropping, due to fragmentation of farms into small holdings of <5 hectares, and intercropping of fodder, vegetables and oil seed crops with cotton is now common practice (Khan and Khaliq 2004; Akram et al. 2011). These plants share many of the same pest and natural enemy species and thus can act as reservoirs or carryover sources to the cotton crop (Godell 2009). Further, pest management practices applied to one plant species can cause direct or indirect effects on pest and natural enemy populations on others (Edwards, 1990). For instance, management of the whitefly *Bemsia tabaci* (Genn.) on alternative hosts prior to the seasonal availability of cotton plants can significantly reduce its carry over to cotton (Attique et al. 2003; Rafiq et al. 2008).

Despite the importance of *A. devastans*, there have been no quantitative reports on its abundance on alternative host plant species that are found within cotton growing areas; previous literature has only reported its occurrence (Huque 1994, Table 1). There is similarly limited information on the occurrence and abundance of natural enemies on alternative host plants (Rao et al. 1968). Here we report for the first time, temporal patterns of occurrence and abundance of *A. devastans* and its natural enemies on a wide range of potential alternative (non-cotton) host plants in cotton growing areas of Southern Punjab, Pakistan. This allows evaluation of the role of non-cotton species in carrying over *A. devastans* populations between cotton growing seasons, their importance in harbouring this pest during the growing season and in maintaining populations of natural enemies.

Materials and Methods

We assessed *A. devastans* and its natural enemies in the cotton agro-ecosystem near Multan in the Punjab province of Pakistan (between 30º11′52″N and 71º28′11″E). Multan is at an altitude of 122m with land area dominated by silt loam soils. It has semi-arid climatic conditions (average rainfall *circa* 186mm) marked by four distinct seasons: a very hot summer (April-June), a wet season in which most of the precipitation occurs with south-western monsoon (July-September) when temperature ranges from 19.5 to 43ºC and a cooler or mild winter (October-March), during which temperature ranges from 4.5 to 34.6ºC (National Oceanic and Atmospheric Administration data 1961-1990) (see also Fig. 1).

Alternative host plant surveys

Exploratory searches were conducted within 100km of Multan. There were a total of 50 visits to each of 42 sites between 1 January and 31 December 2009, with 4 visits in each month except for January in which there were 6 visits to each site. On each survey day, all the available flora inside cotton farmland were examined visually and we also surveyed flora up to 500m outside each cotton field. Plants hosting nymphal and/or adult *A. devastans* were usually identified in the field according to Ali (1982), Ali and Nasir (1991) and Zafar (1996). Any unidentified specimens were taken to the Botany Department of Bahauddin Zakariya University, Multan, for identification by Dr Z.U. Zafar. If *A. devastans* was found on a plant species on at least two survey dates at the same location, the species was considered to be an alternative host. Alternative host plants were further categorized as 'true' host plants if they harboured both nymphal and adult life stages of *A. devastans*, and as 'incidental' host plants if they carried only a few adults for periods of approx. one week at a given location and on which adults were found during at least two survey visits at each site (Mound and Marullo 1996; Froudi et al. 2001). We also noted the availability of identified host plants on each visit throughout the year. Host plants were further assorted for abundance ('abundant' [a large number of the plant species present in all visited locations], 'fair' [found in small numbers in all locations or in large number at few locations] and 'rare' [small numbers at few locations]), plant growth habit or life form (herb, shrub, climber and tree), perenniality (annual, biennial and perennial) and horticultural utility or host type (vegetable, crop, fruit, ornamental and weed) according to a pre-existing system (Attique et al. 2003; Arif et al. 2009; Tiple et al. 2011; Li et al. 2011).

Pest population density estimates

Eighteen of the field sites were selected, on the basis of high host plant availability, from those surveyed in 2009, and were visited at 15 day intervals between January 2010 and December 2011. The prevalence of *A. devastans* on those alternative host plant species which had been found to harbour both nymphal and adult life-history stages in 2009 (i.e. true alternative host plants) was estimated by examining leaves according to the method of Horowitz (1993, see also Leite et al. 2011). Specifically, three leaves were taken from each selected plant; one apical leaf, one leaf from the middle of the plant and one leaf from the lower portion, and the numbers of *A. devastans* nymphs and adults on them were counted. The number of alternative host plants surveyed at each site depended on variation in their abundance (Attique et al. 2003): we sampled from 3 to 33 plants per species per site per visit.

Natural enemy populations

To record predators, whole plant counts (Naveed 2006) were taken from the same true alternative host plant species and from the same sites as selected for population density estimates (see above). The number of plants per sample varied depending variation in abundance (as above); we sampled from 3 to 5 plants per species per site per visit.

To assess the prevalence of parasitoid attack, a total of fifty leaves were removed from each species of alternative host plant present at each site on each visit, taking leaves only from those individual plants that harboured both nymphal and adult *A. devastans* and that could also bear *A. devastans* eggs. These leaves were brought back to the laboratory and a $5cm^2$ diameter leaf discs was cut from the centre of each leaf and placed, on moist filter paper, in a $5cm^2$-diameter petri dish and covered with a lid. Leaf discs were kept at $25 \pm 2^{\circ}C$ and 65%±3% RH until nymphs of *A. devastans* and adult parasitoids emerged. The proportion of parasitism of the *A. devastans* on each leaf disc was calculated as the number of parasitoids emerged divided by the total number of parasitoids plus *A. devastans* (following Naveed et al. 2011): we assumed that all parasitoids belonged to solitary species, as all identified wasps belonged to egg-parasitoid genera which are either exclusively or predominantly solitary (Jepsen et al. 2007; Segoli and Rosenheim 2013).

Statistical analysis

Data analysis was carried out using the GenStat Statistical Package. As population density data were non-normally distributed, non-parametric tests (Kruskal-Wallis, Spearman's rank correlation) were employed to explore the influences of single recorded explanatory variables (Siegel and Castellan 1988). We were constrained to treat all explanatory variables as random effects. Within Kruskal-Wallis analyses, differences between group averages within treatment categories were evaluated by multiple comparisons tests (Siegel and Castellan 1988). Across similar analyses, significance thresholds were adjusted to control type I error rates using the Bonferroni procedure (Quinn and Keough 2002). Proportion parasitism was analysed using logistic ANOVA (Crawley 1993).

Results

Alternative host plant surveys

In 2009, *A. devastans* was recorded from 48 alternative host plant species belonging to 22 taxonomic families (Table 1). Thirty of these species have not previously been recorded as hosts of *A. devastans.* Seven of the alternative host plant species were crops, 5 species were fruit plants, 7 were ornamentals, 17 were vegetables and 12 were weeds. The alternative host plants varied considerably in their growth habit; most were herbs (24 species) with the remainder being climbers (8 species), shrubs (7 species) and trees (5 species). Most of the alternative host plant species were classed as 'abundant' (28 species), followed by 13 'fair' and seven 'rare' plant species in the surveyed area. The majority of the alternative plant species were annuals (32), with only a few perennials (15) and one biennial species (Table 1).

Of the recorded alternative host plant species, 24 were categorized as 'true' host plants as these plants harbour both nymphal and adult life stages of *A. devastans*. As the remaining 24 plant species carried only a few adults for short periods, these were categorized as 'incidental' hosts (Table 1): the remainder of this paper focuses on true alternative host plants.

The availability of true alternative host plants varied through the year. Weeds, fruit plants and ornamentals were typically available throughout the year and crops were mainly available between March and September (Fig. 2). Some vegetable species were present throughout the year (*Abelomoschus esculentus* and *Solanum melongena*) while others were absent for 2 to 6 months: *Pisum sativum* and *S. tuberosum* were absent from April and May, respectively, until October and members of the family Cucurbitaceae (*Citrullus lanatus, Cucumis melo* and *C.*

sativus) were typically absent from around October until around February (Fig. 2); these patterns reflect the annual cycle of cultivation and harvest of each vegetable.

Pest population density estimates

Amrasca devastans population density varied both in time and between true host plant species (Fig. 3). The vegetable *A. esculentus* supported the highest densities of pests. On this species both nymphs and adults were active from March to December, with densities of both peaking around April to May during both 2010 and 2011. In January and February this host species was present but the upper parts had been cut by farmers and *A. devastans* adults and nymphs were absent (Fig. 3). The vegetable *S. melongena* harboured *A. devastans* adults throughout the season from January to December with peak density in November. The presence of multiple nymphal instars throughout the year indicated that breeding took place during all months, but nymphal densities fluctuated greatly and peaked around April to May (Fig. 3). Populations of adult *A. devastans* on *S. tubersum* fluctuated in the same way as for *S. melongena* but the densities of nymphs were very different, with nymphs present only when adults were present, and at very low density (Fig. 3). *Amrasca devastans* was only found on *P. sativum* during March in 2010, and March and January in 2011, but densities were always very low (Fig. 3). The remaining species in the vegetable host type category all showed the same pattern of *A. devastans* abundance, with both adults and nymphs present around May to August and absent in the remaining months of the year (Fig. 3).

The crop species *Ricinus communis* harboured adult and nymphal *A. devastans* throughout the year with adult densities peaking in October and peak nymphal densities in May (Fig. 3). On *Helianthus annus,* adults and nymphal *A. devastans* were present from April to June with maximum densities in April. The remaining crop plant species harboured *A. devastans* from around May until around August (Fig. 3).

Among the weeds, *Xanthium strumarium* supported *A. devastans* adults and nymphal stages throughout the period it was present in the field, with maximum adult densities in November and nymphal densities in August. On *Abutilon indicum*, *A. devastans* adults were found for most periods of the year except February, June and July 2010, and February 2011. Nymphs were present throughout observation period except in June of both years. Both nymphal and adult maximum densities were found in September during both the years. However, the weed *Chenopodium murale* carried overwintering *A. devastans* in January and December. Of the remaining weed species, *A. devastans* was present in low numbers from approximately April to December. Plant species belonging to the fruit or ornamental host type categories carried low densities of *A. devastans* adults and nymphs, with peaks occurring in May or June (Fig. 3).

Estimates of population densities (mean *A. devastans* per leaf) from true alternative hosts did not differ significantly between 2010 and 2011 (Kruskal-Wallis test: H=2.71, d.f.=1, P=0.07) so the data were pooled before further analysis of influence on the average number of *A. devastans* per leaf. Densities of *A. devastans* (nymphs plus adults) were significantly affected by all six of the plant characteristics explored (Table 2). Similarly, when data on nymphal and adult *A. devastans* were analysed separately, there were significant differences in density between plant families (Nymph: H=408.8, d.f.=10, P<0.001; Adults: H=385.8, d.f.=10, P<0.001), with the highest densities on host plants in the family Malvaceae followed by the Euphorbiacae. Species effects were also found when nymphs and adults were analysed separately (Nymph: H=558.6, d.f.=23, P<0.001; Adults: H=548.9, d.f.=23, P<0.001). Multiple comparisons testing indicated that there were no significant differences in nymph or adult numbers between *A. esculentus*, *R. communis* and *S. melongena*, which harboured the highest densities of the pest.

In terms of host plant type, *A. devastans* was most prevalent on vegetables and least common on fruit plants, with densities per plant type category ranging from approximately 0.1 to 1.0 individuals per leaf (Fig. 4). Multiple comparisons testing indicated that while numbers of *A. devastans* differed across crop types overall (Table 2), differences were significant between vegetables, crops and ornamentals, and not also between weeds and ornamentals. Similar overall results were obtained when data on nymphal and adult *A. devastans* were analysed separately (Nymphs: H=44.31, d.f.=4, P<0.001; Adults: H=51.84, d.f.=4, P<0.001).

Amrasca devastans prevalence varied significantly across host growth habits (Table 2) and similar results were found for nymphs and adults when analysed separately (Nymphs: H=59.43, d.f.=3, P<0.001; Adults: H=98.21, d.f.=3, P<0.001). Prevalence was greatest on herbs as compared to shrubs, climbers and trees. Annual plants were found to harbour more adult *A. devastans* than perennial or biennial plants (H=11.38, d.f.=3, P<0.001) while nymphs were more abundant on perennial plants (H=5.97, d.f.=3, P=0.024). For both nymphs and adults, population densities were greater on abundantly distributed plants than on plants with fair or rare abundances (Nymphs: H=95.90, d.f.=2, P<0.001; Adults: H=98.88, d.f.=2, P<0.001).

Populations of *A. devastans* varied significantly between sampling months (H=210.4, d.f.=11, P<0.001) with highest densities observed in May and June (Fig. 1, see also Fig. 3). *Amrasca* *devastans* populations were positively correlated with mean monthly temperature (Spearman's rank correlation test: r_s=0.664, n=12, P=0.005, Fig. 1) and inversely correlated with mean monthly relative humidity (r_s=-0.510, n=12, P=0.022, Fig. 1). Temperature and relative humidity were inversely correlated (r_s=-0.462, n=12, P=0.032, Fig. 1). There was also significant variation across host species during each month (Table 3). *Amrasca devastans* nymphs were most prevalent on *R. communis* from November to March but most prevalent on *A. esculentus* from April to October. Adult *A. devastans* adults were most prevalent on *S. tubersum* from November to January and *R. communis* in February and March. As found for nymphs, adults were more prevalent on *A. esculentus* from April to October (Table 3).

Natural enemy populations

The natural enemies of *A. devastans* found on true alternative host plants comprised both predators and parasitoids. Predatory arthropods were spiders (Order: Araneae) and insects: we recorded *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) [green lacewing], Coccinellid beetles (Coleoptera: Coccinellidae) and two genera of hemipterans: *Orius* spp. (Hem.: Anthocoridae), *Geocoris* spp. (Hem.: Lygaeidae). Possible species within these genera were *O. insidiosius* [minute pirate bug] and *G. punctipes* [big-eyed bug], as both have been previously reported within Pakistani cotton agro-ecosystems (Mari et al. 2007). Among these natural enemies, spiders and coccinellids were the most abundant predators, followed by *C. carnea* (Table 4). Spiders were species in the families Lycosidae and Thomisidae and coccinellid species included *Coccinella septempunctata* (L.), *C. undecimpunctata* (L.), *Hyperaspis maindronii* Sicard, *Scymnous nubilus* Muslant, *Menochilus sexmaculatus* (F.) and *Brumus suturalis (*F.). Dominant (numerically) coccinellids were *C. septempunctata*, *M. sexmaculatus* and *B. suturalis*.

Densities of predators were significantly affected by all six of the plant characteristics explored (Table 2). Plants in the family Euphorbiacae harboured the highest densities of three predators, due to large numbers of spiders, coccinellids and *C. carnea* present on the crop plant *R. communis* (Table 4). Overall, predators were around three times more common on crop plants than on vegetables, and least prevalent on weeds, fruiting plants and the one species of ornamental (Table 4). All five groups of predators were found on most types of alternative host plant, except for fruit plants where *Orius* spp. were the only predators found (Table 4, Fig. 5a). Predators were most common on abundant perennial shrub plants (Tables 1, 4.) The only predator found on rare plants was *C. carnea* (Tables 1 & 4).

All parasitoids found were hymenopterans in the family Mymaridae: *Arescon enocki* (Subba Rao and Kaur) and *Anagrus* sp. These species oviposit in *A. devastans* eggs (Rao et al. 1968; Sahito et al. 2010) that have been laid inside leaf veins (Agarwal and Krishnananda 1976). Overall, *Anagrus* sp. was more common (58.8% of individual parasitoids) than *A. enocki*. The total numbers of parasitoids that emerged were significantly affected by five of the six of the plant characteristics explored but not by the plant's growth habit (Table 2). Parasitoids were most common on perennial plants and emerged from leaves of abundant plant species only (Tables 1, 2, Fig. 6). Parasitoids did not emerge from leaves of weed, ornamental or fruit plant species, but did emerge from three species of vegetables and one species of crop plant (Figs. 5b, 6). Across these four plant species, the overall proportion of *A. devastans* eggs parasitized 0.386 (±0.03 S.E.) and did not differ significantly between plant species (logistic ANOVA corrected for overdispersion: $F_{3,42}$ =2.47, P=0.075, Fig. 6). However, when parasitism by *A. enocki* and *Anagrus* sp. were treated separately, there were significant differences in parasitism across these plant species (*A. enocki*: $F_{3,42}$=21.64, P<0.001; *Anagrus*: $F_{3,42}$=9.82, P<0.001, Fig. 6) due to specialism within vegetable species: *Anagrus* sp. was the only parasitoid to emerge from leaves of *C. melo* var. *phutt* and 83.3% of the parasitoids that emerged from *L. aegyptica* were *Anagrus* sp., while on *A. esculentus* only 13.8% of parasitoids that emerged were *Anagrus* sp.

Discussion

Of the 48 plant species that were found to harbour *A. devastans*, 30 were recorded as alternative hosts for the first time. The other 18 species have been previously recorded by Bhatia (1932), Cherian and Kylasam (1938), Rajani (1940), Husain and Lal (1940), Ghani (1946) and Annonymous (1988). Twenty four of these species can be categorized as true alternative hosts (Mound and Marullo 1996) for *A. devastans*, since they carried both adult and nymphal life-history stages, and constitute the focus of this study (the other species are thus incidental hosts, Froudi et al. 2001).

There was a clear ranking in terms of the importance of different true alternative host plants for *A. devastans*. Species belonging to the families Malvaceae and Euphorbiacae were the most exploited by both nymphs and adults, as also found by Rao et al. (1968); in particular, *A. esculentus* (okra), *S. melongena* (eggplant) and *R. communis* (castor oil plant) harboured the highest densities of *A. devastans*. *Abelomoschus esculentus* is commonly grown near to cotton fields (Baig et al. 2009) and sometimes intercropped with cotton (R.S. pers. obs.). The highest densities of both nymphal and adult *A. devastans* that were observed on this plant in our study, and also in laboratory evaluations (Ghani 1946), may be due to its chemical properties (crude protein, lignin and nitrogen) being particularly favourable for *A. devastans* (Iqbal et al. 2011). Although *A. esculentus* was present in fields throughout the year, it did not support *A. devastans* populations in the months of January or February (see also Eijaz et al., 2012) possibly due to adverse weather conditions (Chiykowski 1981), lower abundance (Power 1987) and plant maturity (Anitha 2007). Despite regular spraying (farmers typically apply insecticides twice per week once pest infestations have become apparent, R.S. pers. obs.), *A. devastans* populations reached high density during April and May. Similar to *A. esculentus*, the vegetable *S. melongena* is typically cultivated in close spatial association with cotton and *A. devastans* also breeds on this alternative host throughout the year, with regular spraying (Yousafi et al. 2013) constituting a possible cause of the observed fluctuations in adult and nymphal densities.

In contrast, *R. communis* is a perennial plant that is cultivated for oilseed on a commercial scale in many countries (Parsons and Cuthbertson 1992); in Pakistan it is grown on a domestic scale on marginal land or near field borders (Hattam and Abbassi 1994). These plants are exposed to relatively little insecticide spray and hence *A. devastans* populations are able to exist on them continuously, with observed fluctuation likely due to the growth stage of the plants and meteorological conditions, as above. These three alternative host plants are thus the main reservoir of *A. devastans* and the primary carry-over source to cotton (see also Huque 1994; Sirivansan 2009).

Although weed species, particularly *A. indicum* and *C. murale*, harbour comparatively low populations of *A. devastans*, their availability throughout the year and potential to harbour refuge populations when cotton is not present (inter-harvest period) suggests that weeds may play a disproportionally important role in influencing pest dynamics.

Our population density studies showed that *A. devastans* persist in the cotton agro-ecosystem throughout the year due to the continuous availability of at least some species of true alternative host plants but the population density on each host plant varied according to its seasonal cycle. These results accord with observations of Setamou et al. (2000) and Barman et al. (2010) who found notable effects of season and growth stage of host plants on population density fluctuation of *Mussidia nigrivenella* (Lepidoptera: Pyralidae) in the maize agro-ecosystem in Benin and of *Lygus hesperus* (Hemiptera: Miridae) in the cotton agro-ecosystem in Texas (USA) respectively.

In the cotton agro-ecosystem we observed, the usage of true alternative host plants by *A. devastans* peaked in May and June, when temperatures were highest and humidity was lowest: high pest densities on preferred alternative host plants are likely to promote local dispersal of *A. devastans* individuals onto other available plant species. In a study of *A. devastans* populations within cotton crops, Naveed (2006) concluded that both warm and humid weather promoted pest population growth: the difference between this and our findings may be due to the differing foci on cotton and non-cotton alternative hosts. In most areas of the Southern Punjab, cotton sowing commonly starts in May (Ali et al. 2011), which coincides with the greatest build-up of *A. devastans* populations. Hence, shortly after cotton seedling emergence, *A. devastans* individuals are likely to migrate from nearby alternative vegetable, crop and weed hosts into the cotton crop, leading to severe infestation and possibly the complete failure of the crop (Ghani 1946). Chemical control is the only tactic being widely used by farmers to protect the cotton crop from *A. devastans* infestation (Razaq et al. 2013). Harmful effects of pesticide usage are well documented by many authors (Zhang et al. 2011; Zidan 2012). Due to excessive and sole reliance on insecticides, *A. devastans* has now developed resistance against pyrethroid insecticides (Ahmad et al. 1999).

In developed countries agriculturalists have reduced pesticide usage by employing biological pest control (e.g. Bari and Sardar 1998; Tscharntke 2000; Thacker 2002; Gray et al. 2009). *Orius* sp., *G. punctipes*, *C. carnea*, Coccinellid spp. and spiders are all common predators of *A. devastans* (Mallah et al. 2001; Vennila at al. 2007). We found the highest numbers of predators on crop and vegetable alternative host plants, especially *R. communis*. *Ricinus communis* may provide a favourable habitat for predatory arthropods due to relative low exposure to pesticides (see above) or because its perennial bushy canopy provides both shelter during adverse environmental conditions and harbours prey throughout the year. Further, *C. carnea* adults feed on *R. communis* pollen (Sattar 2010).

In addition to the predators, two species of egg parasitoids commonly attacked *A. devastans* on some vegetable and crop alternative host plants. Egg parasitoids may be particularly effective in reducing damage by phytophagous species because hosts are parasitized prior to their feeding on the plant (Wajnberg and Hassan 1994). However, our estimate of *A. devastans* parasitism (38.6%) is only slightly greater than an empirically estimated minimum threshold of 32-36% for biological control success (Tscharntke 2000), and we found no evidence for parasitoid attack on other alternative plant species; this casts doubt on whether parasitoid action alone could be sufficient to control *A. devastans* across the agro-ecosystem. *Arescon enocki* was predominant on *A. esculentus* (see also Sahito et al. 2010) and *R. communis* and *Anagrus* sp. was predominant on *C. melo var. phutt* and exclusive *L. aegyptica*. This variation is potentially due to differing availability of nectar or differences in plant volatile profiles or plant morphology (e.g. Micha et al. 2000; Kennedy 2003; Jervis and Heimpel 2005) or plant mediated outcomes to competitive interactions between the parasitoid species (Hawkins 2000; Tscharntke 2000).

Given that there are at least seven species of natural enemies of *A. devastans* present on alternative host pants, there is potential for these predators and parasitoids to suppress *A. devastans* population outside of, and within, the cotton crop. The degree of any suppression will, however, be dependent on many interrelated factors, which include the abundance of the natural enemy populations, the extent and consequences of any competitive interactions between species (intra-guild predation: Rosenheim et al. 1995; Hawkins 2000), the susceptibility of natural enemies to pesticides (Tscharntke 2000) and the potential for the natural enemies to migrate from alternative host plants into the cotton crop during the growing season, and out of the cotton crop at harvest (Tscharntke 2000). Such factors will ultimately determine whether each species of alternative host plant acts more as a source of natural enemies or as a source of *A. devastans*. It is also possible that further plant species (that do not harbour *A. devastans* and are thus not among the 'alternative host plants' we surveyed), could harbour different species of insect herbivores and serve as sources of generalist natural enemies of *A. devastans*, thus additionally influencing the population biology of this pest.

Conclusions and recommendations

In conclusion, our study has shown that alternative host plants can harbour *A. devastans* populations and thus have high potential to act as reservoirs of pest individuals which can then migrate into the cotton crop. These reservoirs will be particularly important during the inter-harvest period, when cotton plants are not present. In this respect the presence of alternative host plants is disadvantageous to the cotton agro-ecosystem but the disadvantage is mitigated in two ways: first, alternative host plants harbour natural enemies of *A. devastans* and, second, many alternative host plants are vegetables, crops and fruits and thus agriculturally beneficial in their own right. The relative pros and cons of their presence in cotton growing areas are thus not straightforward to evaluate, but our results indicate that the characteristics of given species of alternative host plant species, such as type, growth habit, perenniality and abundance, will influence this balance. This evaluation was based on a series of regular field surveys in which the composition and numbers of plant species at each site and survey date, and thus the plant characteristics examined, were not under experimental control. Further work may be required to tease apart the influences of phylogenetically non-independent characters, such as type, growth habit and perenniality.

Given current evidence, we recommend the following actions to reduce damage by *A. devastans* via integrated pest management: (1) Remove alternative weeds host plants from cotton fields and their vicinity. (2) Avoid intercropping and cultivation of the vegetables *A. esculentus* and *S. melongena* in cotton fields, and also avoid growing the perennial *R. communis* near cotton fields or in field margins. Despite harbouring natural enemies, these three species harbour the highest densities of *A. devastans* throughout the year and thus appear to constitute important carryover sources of the pest. (3) Avoid frequent use of pesticides on vegetables: when applications are necessary, use selective insecticides which have minimal effects on natural enemy species. (4) Modify the timing of sowing to desynchronize the period during which cotton plants are in the early seedling stage, and especially vulnerable to *A. devastans* attack, from the peak period of pest density.

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Table 1. Alternate host plants of the *Amrasca devastans* recorded during 2009-2010

Plant characteristics						Results		
Family	**Host plant**	**Vernacular name**	**Host type**[1]	**Growth habit**[2]	**Perenniality**[3]	**New host record**[4]	**Status**[5]	**Abundance**[6]
Amaranthaceae	*Achyranthes aspera* L.	Phuttkanda	Weed	Shrub	Biennial	Yes	True	Abundant
	Digera arvensis Forsk	Diagra, Tandla	Weed	Herb	Annual	Yes	Incidental	Abundant
Apiaceae	*Coriandrum sativum* L.	Dhania, coriander	Vegetable	Herb	Annual	Yes	Incidental	Fair
Asteraceae	*Helianthus annuus* Linn.	Sunflower	Crop	Herb	Annual	No	True	Abundant
	Xanthium strumarium L.	Cocklebur	Weed	Herb	Annual	Yes	True	Abundant
	Gerbera jamesonii Adlam	Gerbera	Ornamental	Herb	Perennial	Yes	Incidental	Rare
Bignoniaceae	*Tecoma stans* Juss.	Tecoma	Ornamental	Shrub	Perennial	Yes	Incidental	Rare
Boraginaceae	*Cordia dichotoma* G. Forst	Lasora	Fruit	Tree	Perennial	Yes	True	Rare
Brassicaceae	*Brassica rapa* L.	Turnip	Vegetable	Herb	Annual	Yes	Incidental	Abundant
	B. compestris var. *sarson*	Sarson	Vegetable	Herb	Annual	Yes	Incidental	Abundant
	Raphanus sativus L.	Radish	Vegetable	Herb	Annual	Yes	Incidental	Abundant
Chenopodiaceae	*Chenopodium murale* L.	Karund	Weed	Herb	Annual	Yes	True	Abundant
	Chenopodium album L.	White goosefoot, Bathoo	Weed	Herb	Annual	Yes	Incidental	Abundant
	Spinacea oleraceae L.	Spinach	Vegetable	Herb	Annual	Yes	Incidental	Abundant
Convolvulacae	*Convolvulus arvensis* L.	Lehli	Weed	Climber	Perennial	Yes	Incidental	Abundant
Cucurbitaceae	*Cucumis melo* L. *var. phut*	Phutt	Vegetable	Climber	Annual	Yes	True	Abundant
	C. melo L. *sativus*	Muskmelon	Vegetable	Climber	Annual	Yes	True	Abundant
	C. sativus L.	Cucumber	Vegetable	Climber	Annual	Yes	True	Abundant
	Citrullus lanatus (Thumb) Mansf.	Watermelon	Vegetable	Climber	Annual	No	True	Fair
	Lagenaria vulgaris Ser.	Gourd, Kaddu	Vegetable	Climber	Annual	No	True	Abundant
	Luffa aegyptica Mill.	Sponge gourd, Tori	Vegetable	Climber	Annual	No	True	Abundant
	Cucurbita pepo L. var. *melopepo*	Squash	Vegetable	Climber	Annual	Yes	Incidental	Fair
Cyperaceae	*Cyperus rotundus* L.	Deela	Weed	Herb	Perennial	Yes	Incidental	Abundant
Euphorbiaceae	*Ricinus communis* L.	Castor oil plant	Crop	Shrub	Perennial	No	True	Abundant
Labiatae	*Ocimum basilicum* L.	Niazboo	Ornamental	Herb	Annual	Yes	Incidental	Rare
Leguminoseae	*Trifolium alexandrinum* L.	Barseem	Crop	Herb	Annual	Yes	Incidental	Fair
Malvaceae	*Abelmoschus esculentus* L.	Okra, Bhindi, ladies' fingers, gumbo	Vegetable	Herb	Annual	No	True	Abundant
	Abutilon indicum Sweet	Mallow, Kanghi	Weed	Shrub	Annual	No	True	Abundant
	Hibiscus rosa-sinensis L.	China rose	Ornamental	Shrub	Perennial	No	Incidental	Rare
	Malvaviscus arboreus Cav. Diss	Cocks comb	Ornamental	Shrub	Perennial	Yes	Incidental	Rare
Moraceae	*Morus laevigata* L.	Shahtoot	Fruit	Tree	Perennial	Yes	Incidental	Fair
Myrtaceae	*Syzgium cumini* L. Skeels.	Jaman	Fruit	Tree	Perennial	Yes	Incidental	Fair
Pedaliaceae	*Sesamum indicum* L.	Sesame, Til	Crop	Herb	Annual	No	True	Rare
Papilionaceae	*Pisum sativum* L.	Peas	Vegetable	Shrub	Annual	No	True	Abundant
	Cyamopsis tetragonoloba L.	Guar	Crop	Shrub	Annual	Yes	True	Fair
	Phaseolus mungo L. Hepper	Rawan	Crop	Herb	Annual	No	True	Fair
Rhamnaceae	*Zizyphus mauritiana* Lamk	Ber	Fruit	Tree	Perennial	Yes	Incidental	Abundant
Rosaceae	*Rosa indica* L.	Rose	Ornamental	Shrub	Perennial	Yes	Incidental	Fair
Solanaceae	*Solamum melongena* L.	Brinjal (eggplant, aubergine)	Vegetable	Herb	Annual	No	True	Abundant
	S. inacum Dunal	Ester white egg plant	Ornamental	Herb	Annual	No	True	Fair
	S. tuberosum L.	Potato	Vegetable	Herb	Annual	No	True	Abundant
	S. nigrum L.	Mako	Weed	Herb	Annual	Yes	Incidental	Abundant
	Nicotiana tabacum L.	Common tobacco	Crop	Herb	Annual	No	True	Fair
	Datura metel L.	Thornapple, Datoora	Weed	Shrub	Annual	No	True	Abundant
	Physalis alkakengi. L.	Mamola	Weed	Herb	Perennial	Yes	Incidental	Abundant
	Capsicum frutescens L.	Chillies	Vegetable	Herb	Annual	No	Incidental	Abundant
	Withania somnifera Dunal	Winter cherry, Aksen	Weed	Shrub	Perennial	Yes	Incidental	Fair
Tiliaceae	*Grewia asiatica* L.	Falsa	Fruit	Tree	Perennial	No	True	Fair

Notes:

[1, 2, 3, 5, 6] Represent the categories of host plants scored according to Mound and Marullo (1996); Attique et al. (2003); Arif et al. (2009); Tiple et al. (2010); Li et al. (2011)

[4] Yes = New alternative host plants in Pakistan with no previous world record; No= alternative host plants previously reported by Bhatia (1932), Cherian and Kylasam (1938), Rajani (1940), Husain and Lal (1940), Ghani (1946), Annonymous (1988)

Table 2. Effects of true alternative host plant variables on population density of *Amrasca devastans* and its natural enemies. Results are from Kruskal-Wallis one-way analyses of variance on pooled numbers of adult and nymphal *Amrasca devastans* and on predators (5 species pooled) and parasitoids (2 species) for 2010 and 2011. Host plant variables are as in Table 1.

Explanatory variable	d.f.	H value	P[a]
Amrasca devastans			
Family	10	426.5	< 0.001
Species	23	586.6	< 0.001
Type	4	50.36	< 0.001
Growth habit	3	89.91	< 0.001
Perenniality	2	9.62	0.003
Abundance	2	97.18	< 0.001
Predators			
Family	10	116.0	< 0.001
Species	23	166.7	< 0.001
Type	4	42.36	< 0.001
Growth habit	3	24.50	< 0.001
Perenniality	2	14.12	< 0.001
Abundance	2	22.98	< 0.001
Parasitoids			
Family	10	23.57	< 0.001
Species	23	37.02	< 0.001
Type	4	3.19	< 0.001
Growth habit	1	1.72	0.018 NS[a]
Perenniality	2	3.79	< 0.001
Abundance	2	3.19	< 0.001

[a] Because 6 tests were carried out for each category of organisms we adjusted the significance criterion, according to the Bonferroni procedure, to be 0.05/6, i.e. <0.0083.

Table 3. Monthly variation in *Amrasca devastans* populations across true alternative host plant species

Data are pooled across 2010 and 2011.

Month	Preferred host plant	Difference across 24 host species		
		d.f.	H	P[a]
Nymphs				
January	*Ricinus communis*	23	71.3	< 0.001
February	"	23	59.9	< 0.001
March	"	23	72.1	< 0.001
April	*Abelomoscus esculentus*	23	114.0	< 0.001
May	"	23	133.6	< 0.001
June	"	23	113.3	< 0.001
July	"	23	114.8	< 0.001
August	"	23	114.3	< 0.001
September	"	23	136.1	< 0.001
October	"	23	90.8	< 0.001
November	*Ricinus communis*	23	83.8	< 0.001
December	"	23	83.6	< 0.001
Adults				
January	*Solanum tubersum*	23	85.9	< 0.001
February	*Ricinus communis*	23	49.9	< 0.001
March	"	23	71.3	< 0.001
April	*Abelomoscus esculentus*	23	134.9	< 0.001
May	"	23	124.0	< 0.001
June	"	23	112.3	< 0.001
July	"	23	123.5	< 0.001
August	"	23	143.3	< 0.001
September	"	23	141.1	< 0.001
October	"	23	84.3	< 0.001
November	*Solanum tubersum*	23	93.4	< 0.001
December	"	23	94.9	< 0.001

[a] Because 12 tests were carried out for each *A. devastans* life history stage we adjusted the significance criterion, according to the Bonferroni procedure, to be 0.05/12, i.e. <0.0042: all results were significant at this more stringent level.

Table 4. Mean numbers of arthropod predators on true alternative host plants. Numbers shown are means from up to 5 plants per species per site per visit, pooled across all sites and across two sampling years.

Host plant type and species	**Predator**					
	***Orius* spp.** Minute pirate bug	***Geocoris* spp.** Big eyed bug	***Chrysoperla carnea*** Green lacewing	**Coccinellid spp.** Lady beetles	***Araneae* spp.** Spiders	**Overall Mean**
Vegetable						
Mean	2.26	1.77	1.34	1.26	3.70	2.06
Abelmoschus esculentus	1.15	0.09	1.42	1.10	5.55	1.86
Citrullus lanatus	0.85	1.35	0.60	0.50	1.75	1.01
Cucumis melo	1.65	0.60	0.50	0.90	1.35	1.00
Cucumis melo var. phutt	5.35	4.25	0.60	1.10	7.50	3.76
Cucumis sativus	0.60	0.75	1.15	1.10	3.10	1.34
Lagenaria vulgaris	7.50	7.50	0	5.00	0	4.00
Luffa aegyptica	3.60	0	0.25	1.00	2.75	1.52
Pisum sativum	0	0	0	0.50	0.35	0.17
Solamum melongena	1.85	3.15	3.85	1.35	9.60	3.96
Solamum tuberosum	0	0	5.00	0	5.00	2.00
Crop						
Mean	2.13	0.23	4.86	7.93	15.31	6.09
Cyamopsis tetragonoloba	0	0	1.15	0	9.15	2.06
Helianthus annuus	0.25	1.35	2.85	2.60	5.10	2.43
Phaseolus mungo	5.00	0	3.75	0	2.50	2.25
Nicotiana tabaccum	0	0	0	0	1.35	0.27
Ricinus communis	7.50	0	11.40	45.00	73.75	27.53
Sesamum indicum	0	0	10	0	0	2.00
Weed						
Mean	0.50	0.67	0.75	2.48	1.00	1.08
Abutilon indicum	0	3.35	0	1.00	0	0.87
Achyranthes aspera	0	0	0	0.09	0	0.02
Chenopodium murale	0	0	0	10.00	0	2.00
Datura metel	0	0	0	0.08	0	0.02
Xanthium strumarium	2.50	0	3.75	1.25	5.00	2.50
Ornamental						
Solamum incanum	0.25	1.00	0.90	0.15	2.75	1.01
Fruit						
Mean	1.25	0	0	0	0	0.25
Cordial dichotoma	0	0	0	0	0	0
Grewia asiatica	2.50	0	0	0	0	0.50
Overall mean	1.69	0.97	1.97	3.03	5.69	2.67

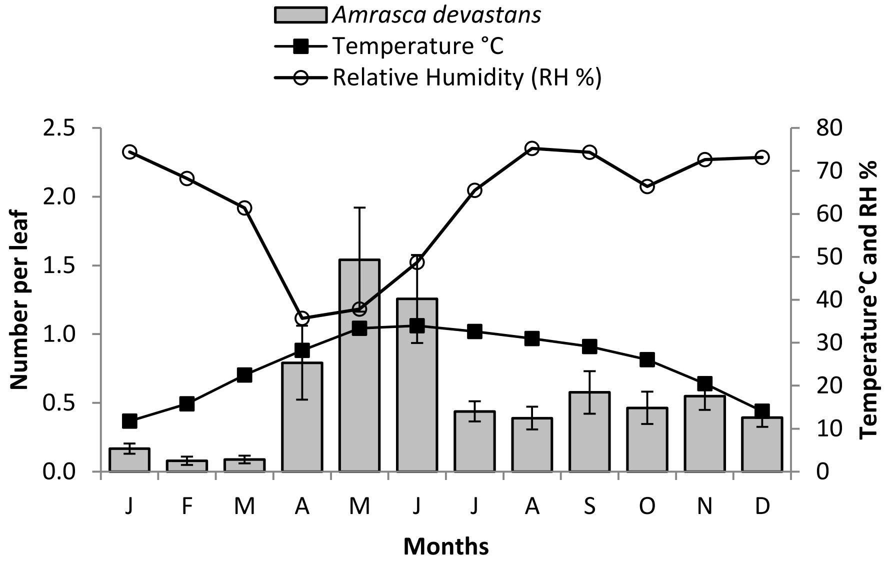


Fig. 1 Seasonal fluctuation (±S.E.) of *Amrasca devastans* on true alternative host plants. All data are pooled across 2010 and 2011. *A. devastans* bars represent nymphs plus adults. Meteorological data were obtained from the Central Cotton Research Institute, Multan

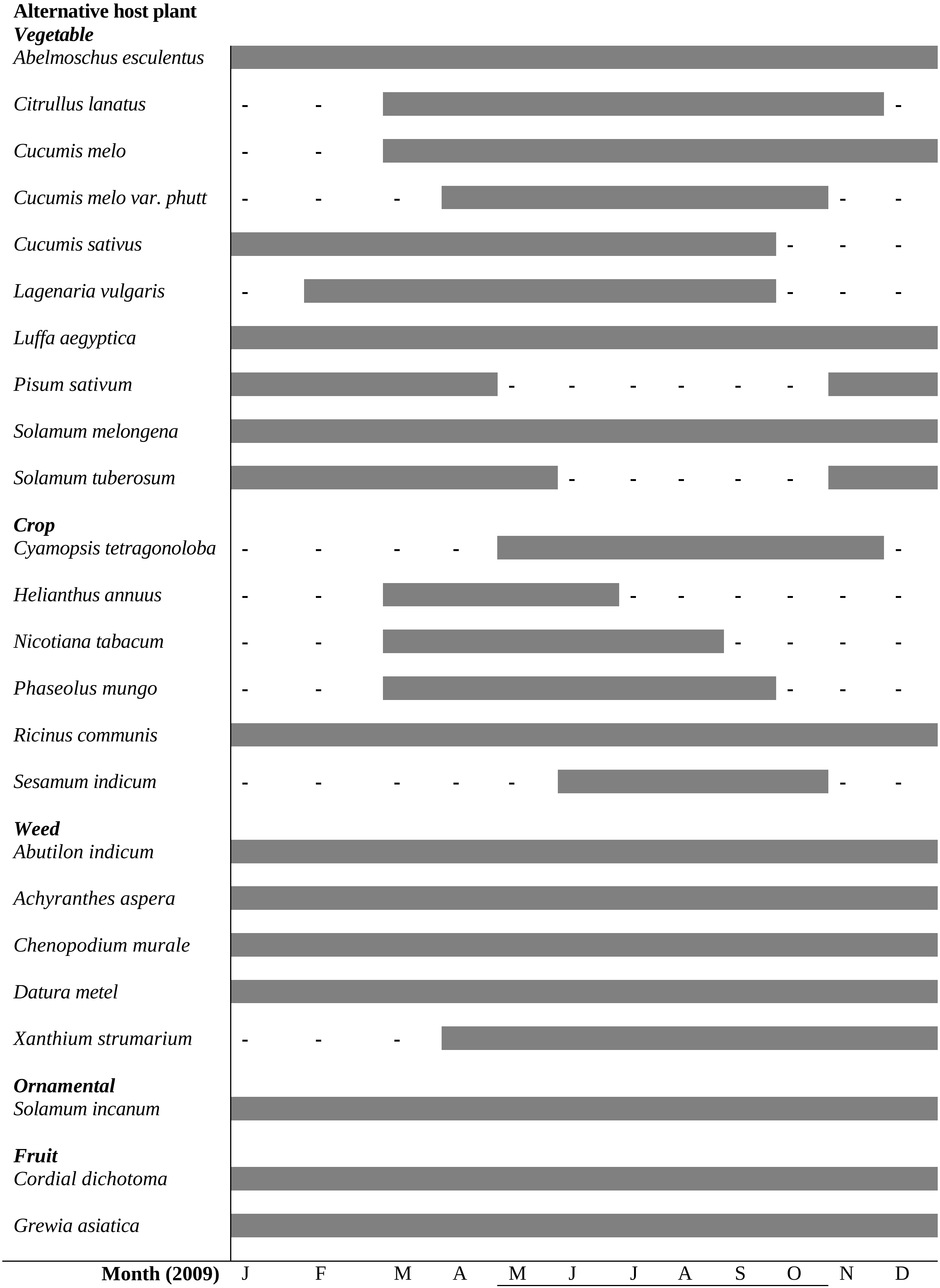


Fig. 2 Temporal availability of true alternative host plants of *Amrasca devastans*. Cotton is commonly sown from early May and remains in the field until harvest in October each year (indicated by line below months)

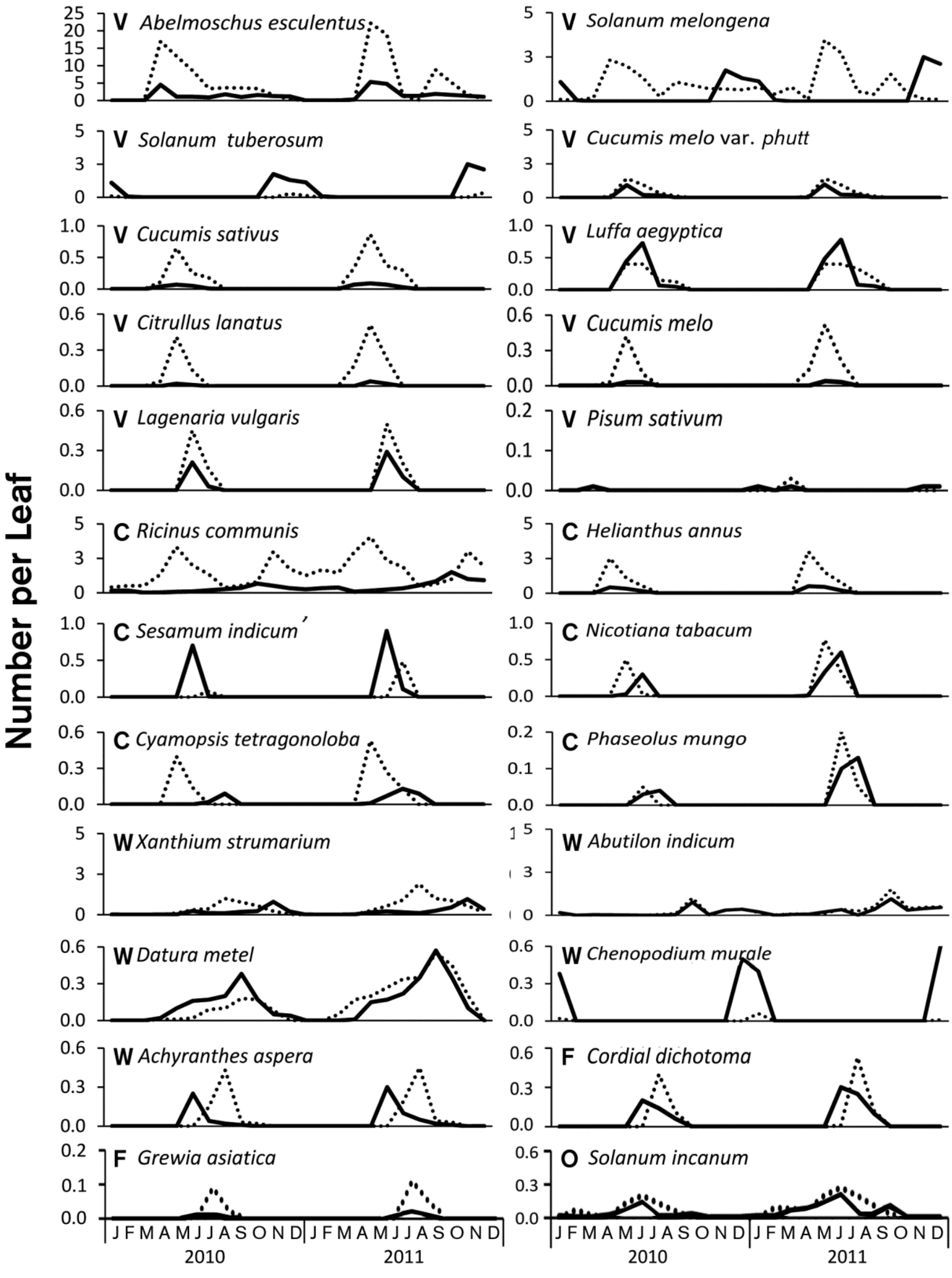


Fig. 3 Seasonal prevalence of *Amrasca devastans* on true alternative host plants. Dotted lines indicate data on nymphs, solid bold lines indicate adults. F, O, C, W and V respectively indicate fruit, ornamental, crop, weed and vegetable plants. Note that different panels have different y-axis scales

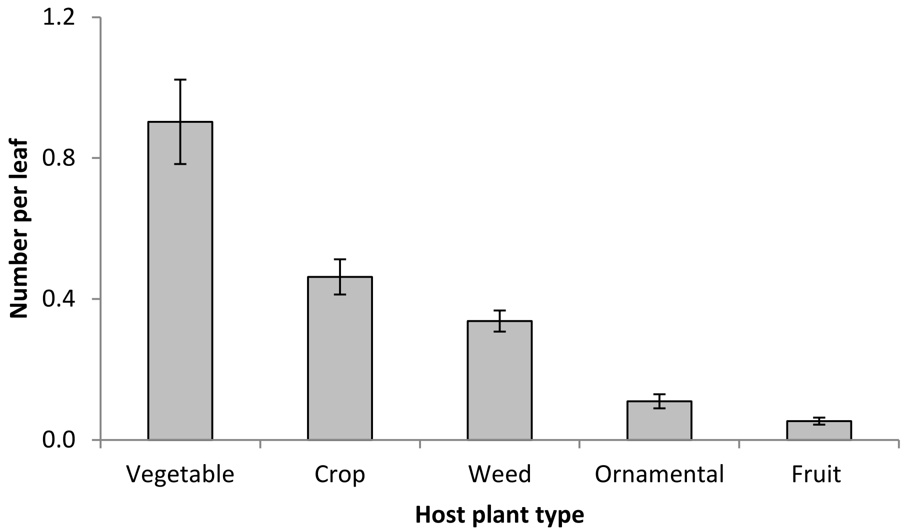
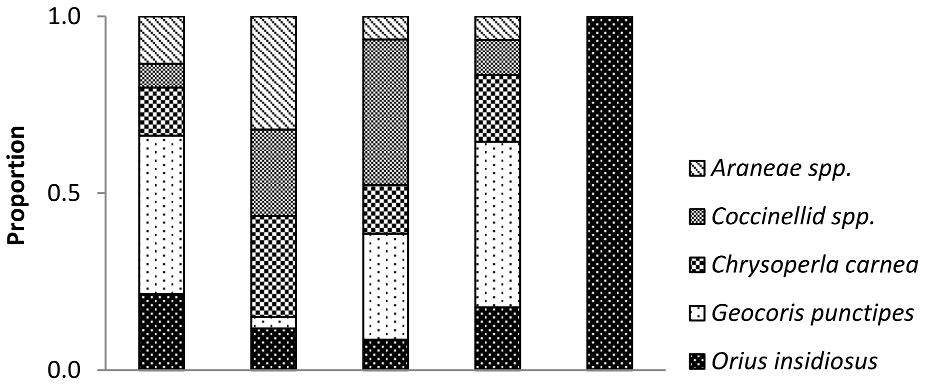


Fig. 4 Mean number (±S.E.) of *Amrasca devastans* on different true alternative host plant types (pooled data for 2010 and 2011, nymphs plus adults). The numbers of *A. devastans* differed significantly across host plant types overall but comparisons were not significantly different between vegetables, crops and ornamentals, and not also between weeds and ornamentals.

(A) Predators



(B) Parasitoids

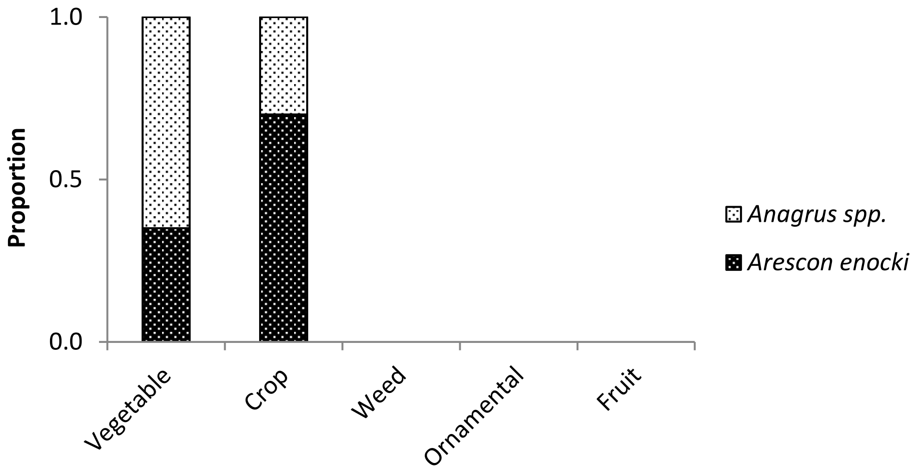


Fig. 5 Contribution of true alternative host plant types for carrying natural enemies of *Amrasca devastans* during the survey period. (A) predators, (B) parasitoids

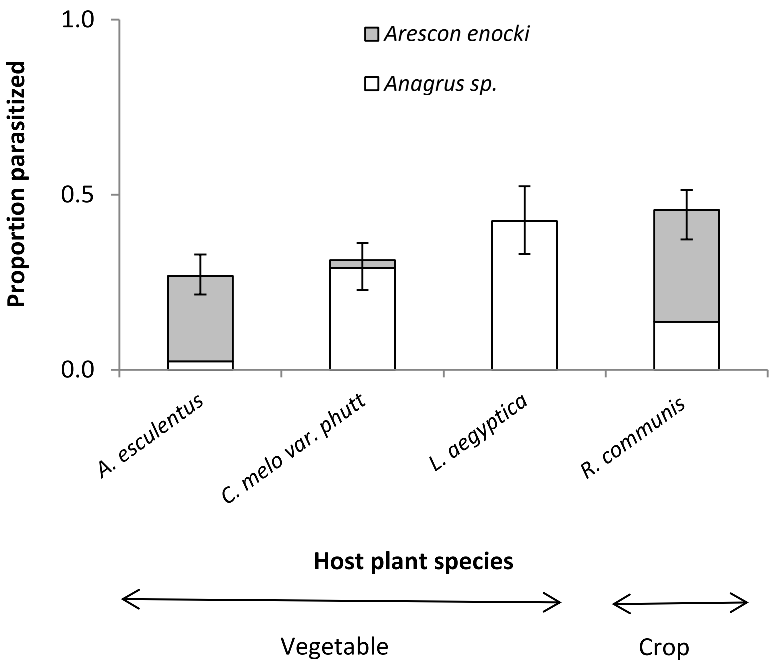


Fig. 6 Mean (±S.E.) parasitism of *Amrasca devastans* eggs laid on true alternative host plant species